Reproduction in Octocorals (Subclass Octocorallia): A Review of Published Literature

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General Reproductive Strategies (Asexual and Sexual)

The Subclass Octocorallia represents a geographically and morphologically diverse group of Cnidarians for which basic life history, including reproductive biology, is poorly known in most species. Current knowledge of reproduction in this group is derived from a few of taxonomic descriptions which include information on reproductive morphology (e.g. Kukenthal 1919), and a limited number of published studies on reproductive biology and ecology in mostly tropical species.

Both sexual and asexual reproduction have been documented in octocorals. The contribution of each form of reproduction to overall population growth appears to vary between species and environments (Lasker 1983; Lasker 1996). Octocorals possess a number of reproductive strategies found in other anthozoans; however, the diversity of mechanisms by which asexual reproduction occurs makes this group unique. Types of clonal propagation found in octocorals include: simple fission (Benayahu and Loya 1985); partial mortality with division into two separate entities (Farrant 1985); survival and reattachment of colony fragments (Lasker 1984, Walker and Bull 1983); development of colonies from stolons or runners (Dineson 1985; Lasker 1983); and rapid autotomy of small fragments with root-like processes (Dahan and Benayahu 1997). In addition, the asexual development of planula via parthenogenesis has been reported for at least two octocoral species (Brazeau and Lasker 1989, Hartnoll 1975).

Studies to date indicate that asexual reproduction in octocorals is most common among tropical “soft corals”, especially in the families Alcyoniidae, Clavulariidae, Nephtheidae, and Xeniidae. Certain gorgonian-type octocorals including Briarium asbestinum, Plexaura kuna, and Juncella fragilis are also known to asexually propagate (Lasker 1983, 1984; Walker and Bull 1983). There is evidence that asexual propagation, via vegetative growth, allows for high population growth rates via rapid colonization of substrate (Benayahu and Loya 1987). Thus, species capable of this reproduction strategy often exhibit high local abundances and an ability to rapidly recover following disturbance (Dahan and Benayahu 1997; Highsmith 1982; Jackson 1985).

There is limited knowledge concerning the effect of asexual reproduction on the sexual reproductive cycle and general fitness in octocorals. Lasker (1990) reported that there is no evidence of a trade-off between sexual reproduction and vegetative propagation in P. kuna. He suggested that for this species, vegetative propagation might be better characterized as a clonal growth strategy as opposed to reproductive strategy. In contrast, McFadden (1991) modeled contributions of asexual and sexual reproduction to relative fitness in Alcyonium sp. and reported that increased fitness was associated with an increase in colony fission at the expense of sexual reproduction.

Asexual reproduction is clearly important for population growth in some alcyonacean corals, however the vast majority of octocorals are known to reproduce only sexually. Most species are gonochoristic (Table 1), although hermaphroditism has been recorded in several Xenid "soft corals" (Table 1). In Heteroxenia fuscescens, colonies display a size-dependant and functional sequential hermaphroditism, a strategy that may represent age-specific reproductive effort for optimal energy allocation (Achituv and Benayahu 1990). Two basic types of sexual reproduction are known in octocorals: (1) broadcast spawning with fertilization and development in the water column; (2) fertilization in or on the maternal colony and subsequent brooding of embryos internally or externally on the adult colony. The frequency of brooding vs. broadcasting spawning in octocorals varies with taxonomic order. Brooding occurs in the sole extant member of the Order Coenothecalia (Babcock 1990) and is common in the Order Alcyonacea (Alino and Coll 1989; Brazeau and Lasker 1989, 1990; Coma et al. 1995; Grigg 1977; Goldberg and Hamilton 1974; Kinzie 1970 and others), but unknown in the Order Pennatulacea whose members appear to exclusively broadcast spawn (Rice et al. 1992, Tyler et al. 1995, and Eckelbarger et al. 1998). Among alcyonacean octocorals the frequency of brooding vs. broadcast spawning appears to vary by group ("soft corals" vs. "gorgonian-type" corals) and by environment (tropical vs. temperate) however, these generalizations are based on a vastly incomplete knowledge of reproduction in this order. Coll et al. (1995) consider broadcast spawning to be the most common sexual reproductive strategy for Alcyonaceans, with brooding occurring most commonly among gorgonian-type corals. A trend toward brooding may also extend to cold-water species (Alino and Coll 1989, Coma et al. 1995) . Cordes et al. (2001) suggest that temperate-water alcyonaceans are more commonly brooders but noted that sexual reproductive strategies vary widely within the same genus (Hartnoll 1975).

At this time it is unclear to what degree reproductive strategies in octocorals are influenced by selective pressures or dictated by phylogenetic constraints; however, it is likely that both brooding and broadcast spawning may each confer certain reproductive advantages, especially in different environments. Alino and Coll (1989) report that many broadcasting spawning octocorals participate in synchronized mass spawning events, a strategy which in reef environments, may yield ecological benefits by reducing predation pressure on newly-spawned gametes. Such highly synchronized spawning events may be critical to reproductive success in broadcast spawners by enhancing fertilization rates (Lasker et al. 1996). Among brooders, spawning synchronicity may not be as crucial, because there is retention of eggs, either inside the polyps or on the colony, surface until fertilization occurs (Coma et al. 1995; Dahan and Benayahu 1997). The surface-brooding, Caribbean octocoral, Pseudopterogorgia elizabethae, is known to achieve relatively high levels of fertilization success despite asynchronous spawning (Lasker unpubl. data in Gutierrez-Rodriguez and Lasker 2004). Babcock (1990) suggests that brooding may be a strategy which compensates for low fecundity by enhancing survival of larval by providing a refuge from predation.

Reproductive Maturity

Octocorals vary in age and size at first reproduction (e.g. Benayahu and Loya 1984a; Coma et al. 1995). Within a species, colony size is a good indicator of

reproductive maturity (Benayahu and Loya 1986; Gutierrez-Rodriguez and Lasker 2004). For example, in Lobophytum crassum, an Alcyonacean "soft coral", colonies that measure < 18 cm across are not reproductive (Yamazato et al. 1981) while in another "soft coral", Heteroxenia fucenscens, colonies do not reach reproductive maturity until colony volume exceeds 10 cm3 (Achituv and Benayahu 1990). In the Caribbean "gorgonian-type" coral, Pseudoplexaura porosa, colonies that are less that 50 cm tall do not contain gonads (Kapela and Lasker 1999) whereas Pseudopterogorgia elisabethae, another Caribbean species, becomes reproductively mature when colonies reach a height of 18-20 cm (Gutierrez-Rodriguez and Lasker 2004).
In colonial marine invertebrates, size-dependant reproduction is relatively common and may represent a strategy whereby resources are allocate to growth at the expensive of reproduction, until a colony reaches a minimize size. By attaining a "threshold" size as rapidly as possible, octocorals may minimize the elevated risk of mortality associated with small colony size (Harvell and Grosberg 1988; Gutierrez-Rodriguez and Lasker 2004; Kapela and Lasker 1999).

Reproductive morphology & Gametogenesis

The basic reproductive anatomy of octocorals is typical of anthozoans. In both sexes, gonads develop along the ventral and lateral (non-asulcul) mesenteries, often in the basal region of the polyp (Achituv and Benayahu 1990; Kruger et al. 1998; Tyler et al. 1995). Germ cells originate in the gastrodermis and are initially surrounded by a layer of mesoglea with overlying gastrodermis (Chia and Crawford 1973; Fautin and Mariscal 1991; Gutierrez-Rodriguez and Lasker 2004). Clusters of primordial germs cells are often attached to mesenteries (or mesentarial filaments in Pennatulaceans) by a short pedicel of "stalk" (Achituv and Benayahu 1990; Farrant 1986; Tyler et al. 1995). Babcock (1990) noted the presence of a "trophonema-like" structure at the oocyte point of attachment to the mesentery in Heliopora coerulea (Order Coenothecalia), a feature which is absent among octocorals but common among actinians (Fautin and Mariscal 1991). Specialized cells of gastrodermal origin, termed "follicle cells" may associated with the developing germ cells (Eckelbarger et al. 1998). The presence of follicle cells during gametogenesis differentiates the developmental process of Anthozoans from other groups within the Cnidaria (i.e. Hydrozoa, Scyphozoa, Actinaria) (references in Fautin and Mariscal 1991). As gonads increase in size, they extend into the polyp cavity. Developing gametogenic cells may be released into the coelenteron before fully differentiated (Order Pennatulacea) (Eckelbarger et al. 1998) or are retained on the mesenteries until the maturation process is complete (Order Alcyonacea) (Benayahu et al. 1988, 1989).

Gametogenesis occurs almost exclusively in autozooids; however, in certain species with dimorphic polyps, gonads may occur in the siphonzooids. In the Alcyonacean genus, Anthomastis, only the siphonozooids contain reproductive structures (Jungerson 1927 in Cordes et al. 2001). Similarly, in Bathyalcon robustum the single autozooid is sterile and the siphonozooids contain the gonads (Bock 1938). In the Minabea robusta and as well as octocorals in the Family Paragorgiidae (Order

Alcyonacea), gonads are present in both autozooids and siphonozooids (Bayer 1973; Utinomi and Imahara 1976).

Oogenesis

The development of oocytes begins when clusters of primordial germ cells divide to form oogonia which become primary oocytes. Farrant (1986) reported that not all primordial oocytes within an ovary develop into oocytes in the Alcyonacean coral, Capnella gaboensis. Young oocytes (~20-22µm diameter) are surrounded by a layer of squamous or cuboidal follicle cells derived from the gastrodermis (Chia and Crawford 1973; Eckelbarger et al. 1998). In one of two published ultrastructural studies on gametogenesis in octocorals, Eckelbarger et al. (1998) reported that primary oocytes in the sea pen, Pennatula aculeata, contain an eccentric nucleus with a single nucleolus, a clear basophilic ooplasm, and numerous pleomorphic mitochondria. This study also noted that the region between oocyte surface and associated follicle cells is occupied by acellular mesoglea which increases in thickness with as oocyte grows. The thickness of the follicle cell layer also increases with oocyte development (Eckelbarger et al. 1998) and is ciliated in most studied species (e.g. Benayahu and Loya 1983; Eckelbarger et al. 1998). The oocyte surface may be covered by numerous microvilli which may perform a mechanical protection (Larkman and Carter 1984) or nutritive function (Benayahu et al. 1989).

As oocytes mature, vitellogenesis is initiated. In the sea pen, Umbellula lindahi, this process begins when oocytes reach 150 µm in diameter and are surrounded by a thick layer of follicle cells (Tyler et al. 1995). Although there is no direct evidence that follicle cells are associated with yolk synthesis, indirect evidence from ultrastructural studies, suggests that these cells may function in vitellogenesis (Eckelbarger et al. 1998). The process of vitellogenesis in the Pennatulid octocorals, P. aculeata, involves extensive heterosynthetic lipid synthesis (Eckelbarger et al. 1998). Membrane-bound vesicles (0.5 to 1.0 µm in diameter) coalesce in the ooplasm to form lipid droplets up to 10 µm in diameter, eventually filling the ooplasm (Eckelbarger et al. 1998). The production of lipid in P. aculeata oocytes is unique among invertebrates because this process does not appear to involve any ooplasmic organelles, however lipid droplets are present in neighboring follicle cells (Eckelbarger et al. 1998). Oocytes with high lipid content have been reported in other octocorals including the sea pen, Ptilosarcus gurneyi (Chia and Crawford 1973), the alcyonacean coral Alcyonium glomeratum (Schafer and Schmidt 1980), and several unidentified species of bamboo corals (Family Isididae) (personal observation).

Mature Egg Structure and Size

When a mature oocyte reaches its final size several changes occur. Most notably, the line between the germinal vesicle and the cytoplasm disappears along with the distinct nucleolus (Orejas et al. 2002). Farrant (1986) noted that ultrastructural features of mature oocytes in the Alcyonacean coral, Capnella gaboensis, are similar to those found in Hydra sp. including cortical lipid globules and yolk spheres, numerous

mitochondria, rough ER, Golgi complexes. The surface of mature octocoral eggs may be structurally complex (Fautin and Mariscal 1991). In the Pennatulid P. aculeata, oocytes are covered by numerous branching microvilli that are individually associated with loose bundles of microfilaments (Eckelbarger et al. 1998). Endocytotic pits are also present between microvilli this species. In the Alcyonacean octocoral, Parerythropodium fulvum fulvum, flagella arising from small pits and are surrounded by elevated folds of the cell surface forming a palisade arrangement (Benayahu and Loya 1983), a typical formation in octocorals (Fautin and Mariscal 1991).
The presence of large yolky eggs (~300-1000µm in diameter; see Table 1) is characteristic of octocorals (Hartnoll 1975, Kruger et al. 1998; Orejas et al. 2002), although, mature egg size varies between species (Achituv et al. 1990; Gutierrez-Rodriguez and Lasker 2004; Schleyer et al. 1997). A number of factors have been proposed to account for this inter-specific variation including: reproductive strategy/mode, fertilization success (Kruger et al. 1998), polyp size (Brazeau and Lasker 1990), and larval development (Richmond 1987). For many studied species it is unclear to what degree one or more factors influence egg size, making it difficult to determine any possible ecological significance of oocyte size variation among octocorals. Moreover, certain factors, such as reproductive strategy/mode and fertilization success, have apparently complex relationships to egg size. For example, Orejas et al. (2002) noted that brooding species with internal fertilization generally have large oocytes (>600µm) while Levitan (2000) suggested that in turbulent environments broadcast spawning species with large egg size would be favored because they present a larger target for sperm, increasing the probability of fertilization (Levitan 1993, 1996). Surface brooders, such as Pseudoptergorgia elisabethae, may have relatively small oocytes (300-580 µm) because this reproductive strategy enhances the probability of fertilization for smaller eggs by exposing them to the large volume of water flowing past a colony (Gutierrez-Rodriguez and Lasker 2004).

Polyp size ultimately places a constraint on gonad volume and planula-size in internally brooding species (Brito et al. 1997); but egg size varies between different species even when polyp size is similar (Gutierrez-Rodriguez and Lasker 2004). One factor which may influence final oocyte size is the type of larval development. In octocorals, larger eggs are associated with species that have non-feeding (lecithotrophic), non-pelagic larvae (Hartnoll 1975; Orejas et al. 2002; Cordes et al. 2001). Furthermore, greater nutrient stores associated with larger eggs (Wallace 1985) may be required for larvae with prolonged development to reach maturity, especially in those species with azooxanthellae planula (Coma and Lasker 1997;Gutierrez-Rodriguez and Lasker 2004). Production of large eggs is energetically costly. Harrison and Wallace (1990), Gutierrez-Rodriguez and Lasker (2004) and other authors have suggested that longer periods of oogenesis might be required for the production of larger eggs; however egg size does not seem to be clearly related to length of oogenic cycles in octocorals (Benayahu and Loya 1983, 1984b, 1986). Kruger et al. (1998) argue that large oocytes are commonly found in "soft corals" regardless of whether the development period spans 12-24 months. Furthermore, certain scleractinian corals with relatively small eggs are known to have long oogenic cycles (Fadlallah and Pearse 1982). Benayahu and Loya (1986) proposed that large egg size is not necessarily associated with prolonged oogenesis, but rather with

species having high fecundity, synchronized maturation of gametes and brief periods of spawning. Further studies may be necessary to better resolve the relationship between mature egg size and length of oogenesis.

Fecundity (Polyp Level & Colony Level)

Octocorals vary with regard to both individual polyp and whole colony fecundity. Egg production differs with species, with "gorgonian-type" corals generally having fewer oocytes per polyp than "soft corals" or "sea pens". For example, the Antarctic gorgonian, Thouarella variabilis produces only a single mature egg in each polyp (Brito et al. 1997) while Plexaura kuna, a Caribbean gorgonian, has an average of 1.9 oocytes per polyp (Brazeau and Lasker 1989). In contrast, "soft corals" such as the Sarcophyton glaucum may contain 25-35 oocytes/polyp (Benayahu and Loya 1986) while a Pennatulid octocoral, Ptilosarcus guerneyi, has an average of 20-25 eggs per polyp (Chia and Crawford 1973). Brazeau and Lasker (1989) suggested that relatively low per polyp egg production in "gorgonian-type" octocorals may be due to space limitations within polyps arising from the less flexible nature of the body plan (rigid axis and polyp armature). While polyp size may ultimately limit gamete production (Coma and Lasker 1992), per polyp egg production within a species may vary with the length of the polyp cavity (Benayahu and Loya 1984a). Branch order or size is another common factor influencing fecundity in octocorals (Brazeau and Lasker 1990, Coma et al. 1995, Orejas et al. 2002). Most often, polyps in apical and medial regions of the colony have greater reproductive output than polyps in more distal regions (Brito et al. 1997, Orejas et al. 2002); however, in the Mediterranean gorgonian, Paramuricea clavata, fecundity is higher among distal polyps (Coma et al. 1995). Several authors have suggested that variability in reproductive output among different regions of a colony may be due to differential prey capture rates related to differences in water flow (Soong and Lang 1992). Regions of a colony that capture more food may translate the added nutrition into higher reproductive effort (Orejas et al. 2002). Alternatively, polyps in different regions of a colony may have in various functions (Brito et al. 1997, Hughes 1989). For example, lower branch order polyps (basal) may invest more in growth than reproduction (Orejas et al. 2002) relative to polyps in other regions of the colony. This may also be the case for polyps near the growth tips of branches.

Both polyp and colony level fecundity generally increase with size in octocorals (Gutierrez-Rodriguez and Lasker 2004, Kapela and Lasker 1999), with large colonies contributing disproportionately to egg production within a population (Coma et al. 1995, Beiring and Lasker 2000). Within a species, increasing fecundity with size may result from an increased number of polyps per colony as well as an increase in polyp level reproductive output (Beiring and Lasker 2000), possibly from a shift in resource allocation from growth to reproduction once a colony has reached a size-refuge threshold (Beiring and Lasker 2000). Similarly, inter-specific differences in fecundity are related to both the number of oocytes produced per polyp as well as the number of reproductive polyps contained in a colony.

In Anthozoans, reproductive strategy was once thought to influence polyp-level fecundity where brooding species invested in a few large eggs and parental care while broadcasting species produced higher number of smaller eggs which were released into the water column prior to fertilization (Rinchevich and Loya 1979); however, there is currently little evidence to support this pattern (Brazeau and Lasker 1989, Cordes et al. 2001). Orejas et al. (2002) observed the polyp level fecundity seems to be inversely correlated with population density in benthic cnidarians including the Pennatulids, P. guerneyi and U. lindahli, as well as the Antarctic gorgonian, Ainigmaptilon antarcticum. In the deep-sea, octocorals do not always appear to follow the general pattern of low fecundity. In one of two studies to date on the reproductive biology of a deep-water "soft coral", Cordes et al. (2001) reported that Anthomastis ritteri, exhibits relatively high fecundity and a brooding strategy, whereas P. kuna produces few large oocytes and is a broadcast spawner (Brazeau and Lasker 1997).

Spermatogenesis

Similar to oogenesis, spermatogenesis originates within the mesentarial mesoglea. Sperm cells develop within spherical cysts that are surrounded by a layer of gastrodermally-derived follicle cells in most octocorals. Eckelbarger et al. (1998) report that in P. aculeata, follicle cells are cuboidal and flagellated, and contain lipid droplets, various vacuoles, and heterogeneous inclusions. Unlike the follicular layer associated with developing oocytes, there is little thickening of this often irregular layer with during spermatocyte development (Eckelbarger et al. 1998). Within each cyst, germ cells undergo relatively synchronous development (Achituv and Benayahu 1990) but in many species, spermaries in different developmental stages may exist in the same polyp (Achituv and Benayahu 1990; Cordes et al. 2001; Gutierrez-Rodriguez and Lasker 2004; Kruger et al. 1998 and others). In the earliest stages, spherical spermatogonia (~8-10 µm in diameter) may either line the inner walls of the cyst (Brazeau and Lasker 1990; Rice et al. 1992; Eckelbarger et al. 1998) or uniformly fill the interior (Achituv and Benayahu 1990; personal observation). Ultrastructural studies of P. aculeata reveal that early stage spermatocytes contain a prominent nucleus with eccentric nucleolus and sparse cytoplasm (Eckelbarger et al. 1998). Later stage spermatocytes exhibit a well defined nuclear envelope, a single plaque of heterochromatin, one or more Golgi complexes, and perinuclear mitochondria associated with the outer nuclear envelope (Eckelbarger et al. 1998). As spermatocytes develop into spermatids (~4.0-5.0 µm in diameter), the spherical cells become flagellated and form a radially arrangement along the periphery of the cyst wall with their flagella extending toward cyst center (Cordes et al. 2001; Rice et al. 1992; Achituv and Benayahu 1990; Eckelbarger et al. 1998). In the final stage of development, spermatids differentiate into mature spermatozoa. Chia and Crawford (1973) report that the head of a mature sperm is oval (1.5µm long and 1.0 µm diameter) whereas the head of another Pennatulid octocorals, P. aculeata, is conical (2.6 µm long) (Eckelbarger et al. 1998). Fully mature spermatozoa may remain in a radially arranged (with flagella extending into the cyst center) (Eckelbarger et al. 1998) or be redistributed throughout the cyst as observed in Pseudopterogorgia elisabethae (Gutierrez-Rodriguez and Lasker 2004). In the Alcyonacean octocoral, H. fuscencens, sperm are arranged into bundles within a spermary. In octocorals, spermaries may rupture in the coelenteron,

releasing free sperm through the polyp opening (Brazeau and Lasker 1990). Alternatively, in P. aculeata, intact sperm cysts are released into the water column where they may function as spermatophores (Eckelbarger et al. 1998).

Reproductive Cycle

In octocorals, production of gametes varies widely in duration and synchronicity between species. Generalized statements regarding reproductive cycles in octocorals are somewhat difficult to make due to the highly variable nature of reproductive characteristics, even within a single genus (e.g. Alcyonium; Hartnoll 1975; Sebens 1983). Furthermore, our knowledge of reproduction is currently limited to studies of just a few dozen of the more than 2000 known species. While cognizant of the potential inadequacies associated with generalized descriptions of octocorals reproductive cycles, the following two trends are commonly exhibited by many of the species studied to date: (1) tropical, broadcasting spawning octocorals display synchronous maturation and spawning of gametes (Alino and Coll 1989; Fitzsimmons-Sosa et al. 2004; Benayahu and Loya 1984a; Benayahu et al. 1990, and others); (2) temperate brooding species possess asynchronous gamete development and a protracted spawning period (Coma et al. 1995; Cordes et al. 2001; Sebens 1983, and others). From these trends it clear that reproductive cycles appear to be generally related to both reproductive strategy and as well environment (tropical vs. temperate). The gametogenic and spawning cycle of alcyonacean soft-coral, Sarcophyton glacum, exemplifies the reproductive cycle common to tropical, broadcast spawning octocorals. This species produces large oocytes (500 – 750 μm) which require two years to reach maturity. The presence of two size cohorts of developing oocytes allow female colonies to release the larger, mature cohort during a brief (usually one night), annual spawning event. In contrast, the temperate-water alcyonacean, Anthomastis ritteri, exhibits a reproductive cycle typical of non-tropical, brooding octocorals. Gametogenesis in A. ritteri is continuous, with all developmental stages of gametes simultaneous present. In the laboratory, this species appeared to exhibit nearly continuous reproduction, with apparently temporally random periods of spawning and larval release (Cordes et al. 2001). Cordes et al. (2001) suggest the nearly continuous cycle of reproduction in A. ritteri could also result from “overlapping seasonal cycles of oogenesis” like those found in the tropical alcyonacean Anthelia glauca (Kruger et al. 1998); however periodic examination of gonadal development from in situ colonies will be necessary to confirm the existence and nature of the apparent continuous reproductive cycle in this species (Cordes et al. 2001).

Like many temperate-water, brooding alcyonacean corals, Pennatulid octocorals, appear to have continuous or nearly continuous, reproductive cycles. Based on the presence of gametes in all stages of development, Eckelbarger et al. (1998) suggested that continuous reproduction is a likely strategy for Pennatula aculeate in the Gulf of Maine . Similarly, Rice et al. (1995) found no evidence of periodic or seasonal spawning in the deep-sea Pennatulid, Kophobelemnon stelliferum from the Porcupine Seabight. Unlike all known sea pens and temperate-water, brooding alcyonaceans, there is evidence that the deep-water gorgonian-type alcyonacean, Acanella arbuscula, may exhibit a seasonal reproductive cycle, as evidenced by seasonal gametogenetic development (Lawson

1991). The study of the reproductive biology in this species is the first and only of its kind to date in deep-water gorgonian-type octocoral. No developing embryos or brooded larvae were found in A. arbuscula polyps, nevertheless, Lawson (1991) suggested that this species is most likely a brooder like many shallow-water gorgonian-type octocorals. There is a need for further investigation into the reproductive biology of the vast but relatively unknown deep-water octocoral fauna that populate canyons, seamounts, ocean ridges, and other areas of the world's oceans.

The reproductive cycles of many octocoral species do not obey previously described patterns/trends. For example, the living fossil coenothecalian, Helipora coerulea, is a tropical brooder with synchronized annual gametogenic development and reproduction (Babcock 1990). Similar synchronization in reproductive cycle has been reported for the temperate-water, broadcast spawning alcyonacean, Alcyonium digitatum (Hartnoll 1975). In an alternative reproductive cycle, many shallow-water, gorgonian-type octocoral exhibit prolonged reproductive periods with continuous gametogenesis throughout the months of spawning (Coma et al. 1995; Brazeau and Lasker 1990; Gutierrez-Rodriguez and Lasker 2004). Excoffen et al. (2004) noted that the reproductive cycle of many gorgonian-species includes a "pattern of oocyte development in which a pool of intermediate-size oocytes is maintained throughout the year.." (Brazeau and Lasker 1989 and others). Zeevi and Benayahu (1999) suggest that the group of intermediate-size may be generated by rapid development of primary oocytes followed by continuous and slow maturation of the oocytes.

In nearly all studied species of octocorals, the process of spermatogenesis occurs more rapidly than oogenesis (Coma et al. 1995; Kapela and Lasker 1999 and others), owing to the larger energetic investment in large, yolky eggs. Thus, the onset on spermatogenesis may lag that of oogenesis by many months (Harrison and Wallace 1990) especially in species with highly synchronized spawning events (Babcock 1990; Benayahu and Loya 1986; Kapela and Lasker 1999). In brooding octocorals such as the Caribbean gorgonian-type alcyonacean, Pseudopterogorgia elizabethae, which possess a lengthy spawning period (November – January), spermaries in several stages of development may be present in a polyp (Gutierrez-Rodriguez and Lasker 2004) allowing for asynchronous maturation of sperm in concert with oocyte maturation cycles.
The manufacture of reproductive products is energetically costly. Nutritional control of gametogenesis has been recorded for a wide variety of invertebrates (Giese and Kanatani 1987). There is evidence that timing of gametogenesis and spawning in some octocorals may be strongly influenced by periods of food availability. In the temperate-water alcyonacean Alcyonium digitatum, Hartnoll (1975) reported that gametogenetic development occurs during the early spring and summer when planktonic food sources are most abundant. Spawning in this species occurs in mid-winter and larvae have a prolonged planktonic stage followed by settlement and metamorphosis in time to profit from increased food resources during the spring bloom (Hartnoll 1975). Dahan and Benayahu (1997) suggest that the energetic requirements for year-round gametogenesis in the azooxanthellate alcyonacean, Dendronephtya hemprichi are supplied by two persistent phytoplankton blooms in the Red Sea population at Eilat. Similarly, planulation in the Red Sea gorgonian Acabaria biserialis occurs after a major seasonal

phytoplankton bloom. Zeevi Ben-Yosef and Benayahu (1999) suggest that observed inter-annual variation in reproductive output in this species may be due to year-to-year variation in phytoplankton availability. Lawson (1991) suggests the seasonal cycle of gametogenesis in the deep-water gorgonian octocoral, Acanella arbuscula, may be fueled by the seasonal flux of surface derived organic material to the deep sea.

Food availability has been shown to influence reproductive cycles in some octocorals. Conversely, several authors have noted that reproductive cycle may affect the feeding ability of octocoral polyps. Babcock (1990) reported that mature oocytes in H. coerulea almost complete obstruct the coelenteron and must limit or preclude polyp feeding when mature oocytes are present. In the Antarctic gorgonian-type octocoral, Thouarella variabilis, a single internally brooded larvae may occupy as much as 80% of the volume of the polyp cavity (Brito et al. 1997) leaving little or no space for captured food and digestive processes. The temperate-water alcyonacean, Alcyonium digitatum exhibits a unique behavior during the final few months of gamete development. This species enters a quiescent, non-feeding period from September – November/December during which time the nearly mature gonads are present (Hartnoll 1975).

Spawning & Fertilization Biology

Octocorals vary in both in frequency and degree of synchronicity of spawning events. Broadcasting spawning species maintain highly synchronous gamete release in an effort to: (1) maximize fertilization rates by minimize sperm limitation and; (2) reduce impact of predators on reproductive products by overwhelming their capacity to feed (Alino and Coll 1989: Lasker et al. 1996). Among brooding octocoral species, spawning behavior may be synchronous or asynchronous. A spawning strategy common to many brooders involves a prolonged reproductive season with synchronized monthly periods of gamete release (Benayahu and Loya 1983; Brazeau and Lasker 1990: Coma et al. 1995). In shallow-water octocorals, spawning behavior coincides with lunar cycles, with gamete release occurring at or following full moons (Alino and Coll 1989; Babcock 1990; Brazeau and Lasker 1989, 1990, Coma et al. 1995, Kruger et al. 1998), around or following the new moon (Babcock 1990; Coma et al. 1995) and even preceding the last quarter (Benayahu and Loya 1983). Other factors that may serve as spawning cues including water temperate change (Alino and Coll 1989; Dahan and Benayahu 1997), tidal cycle (Alino and Coll 1989), food fall/delivery (Brito et al. 1997; Lawson 1991), and genetic factors (i.e. internal/biological clock). Asynchronous spawning has been reported for the Caribbean , surface-brooding, gorgonian-type octocoral, Pseudopterogorgia elisabethae (Gutierrez-Rodriguez and Lasker 2004). This species releases the bulk of its gametes during a several 2-10 day periods following new moons from November until early January. Despite spawning asynchrony, Gutierrez-Rodriguez and Lasker (2004) observed high fertilization rates in this species which they suggest may be due to the retention of eggs on maternal until fertilization is achieved. Fertilization may either occur externally in the water column (Dendronephthya hemprichi, Dahan and Benayahu 1997; Pseudoplexaura porosa, Kapela and Lasker 1989; Plexaura flexuosa, Beiring and Lasker 2000, and others) or on surface of the maternal colony (Capnella gaboensis, Farrant 1986; Pseudopterogorgia elisabethae, Gutierrez-

Rodriguez and Lasker 2004 and others) or internally within the female polyp cavity (Anthelia glauca, Kruger et al. 1998; Briarium asbestinum, Brazeau and Lasker 1990; Parerythropodium fulvum fulvum, Benayahu and Loya 1983; Helipora coerulea, Babcock 1990 and others). Alino and Coll (1989) reported that fertilization of gametes in the water column occurred mostly within 30 minutes of release during a mass spawning event on the Great Barrier Reef . Little data is currently available on the length of time required for fertilization among surface and internal brooders.

The process of fertilization was studied in detail for the alcyonacean octocoral, Heteroxenia fuscencens by Gohar and Roushdy (1961). They observed that sperm entered the polyp through the mouth and fertilized the egg while it was still enclosed by a follicular epithelium. Sperm actively "bore" through the follicular layer, entering the mature oocyte either in the location of the "enterance cone" or where the nucleus protrudes. The mechanism of sperm penetrate is not known, though usually only one and occasional more than one sperm penetrate the follicular epithelium and travel to the site of the nucleus where only a single sperm enters. Fusion of the male pronucleus with that of the oocyte results the formation of a kidney-shaped zygotic nucleus, and subsequent thickening of the zygote's mesogleal coat which, together with the external follicular layer, forms a capsule around the early-stage, developing embryo.

The rate of successful fertilization in octocorals appear to be strongly influenced by the position of male colonies in relation to female colonies in a population (Coma and Lasker 1997). Coffroth and Lasker (1998a) found that in the Caribbean broadcast-spawning gorgonian, Plexaura kuna, male reproductive success was determined more by close proximity to female colonies than by over clone size. Similarly, in the Caribbean brooding gorgonian, Briarium asbestinum, Brazeau and Lasker (1992) reported a "significant positive correlation between female reproductive success and the density and proximity of nearby males…"

Given the apparent strong relationship between spatial distribution of males and female colonies within a population, and fertilization success, it is reasonable to infer that the sex ratio within a population may have impact on reproductive success. Sex ratios may vary from 1:1 (e.g. Coma et al. 1995; Kruger et al. 1998; Orejas et al. 2002), 2.2:1 in favor of male colonies (Brazeau and Lasker 1990), to all female among populations (Brazean and Lasker 1989) in different octocoral species. Santangelo et al. (2004) reported that in an over-exploited population of the precious coral, Corallium rubrum, in the Mediterranean , the sex ratio was significantly biased towards females. Selective removal of coral colonies through harvesting or episodes of natural or human-induced disturbance which cause mortality of coral colonies could affect the ability of populations to reproduce by altering the sex ratio of a population.

Factors such as synchronous spawning behavior, oocyte brooding, and proximity of male to female colonies have all been shown to influence fertilization success. Additionally, there is evidence that octocoral oocytes contain chemical compounds, such as (-)-epi-thunbergol, that act as sperm attractants (Coll et al. 1995), and may enhance the ability of male gametes to locate fully mature eggs. Coll and Kelman (1997) identified

small vesicles near the surface of oocytes in the alcyonacean soft Lobophytum crassum that appear to contain a sperm chemo-attractant compound. They suggest that these structures rupture during the process of spawning, releasing the sperm attracting compound.

Embryology & Larval Development

In octocorals, embryos develop into planular larvae. The transition from zygote to the larval stage occurs in less than a week for most studied species (Alino and Coll 1989; Babcock 1990; Gutierrez-Rodriguez and Lasker 2004; Uehara et al. 1987 and others). The rate of this developmental change may be influenced by water temperature, especially in temperate regions (Hartnoll 1975; Dahan and Benayahu 1998). The planular larvae of broadcast spawning corals develop in the water column (Alino and Coll 1989; Chia and Crawford 1973) while the larvae of brooders are retained on or in the parent colony until mature (Benayahu 1989; Kruger et al. 1998; Excoffon et al. 2004 and others). In both brooding "gorgonians" and "soft corals", larvae may be incubated in a mucus coat on the colony surface (Coma et al. 1995; Gutierrez-Rodriguez and Lasker 2004; Benayahu and Loya 1983), in the adult polyp cavity (Benayahu 1991; Brito et al. 1997), or in specialized brood chambers, as is the case for all Xenia spp. (Achituv et al. 1992) and Heliopora coerulea (Order Helioporacea) (Babcock 1990). In octocorals with dimorphic polyps, such as Heteroxenia fuscescens and Heteroxenia coheni, planula may complete develop in the siphonozooids (Benayahu et al. 1989; Benayahu 1991). While the soft coral, Anthelia glauca, from South Africa waters, possess a unique pharyngeal brood pouch for developing embryos and larvae (Kruger et al. 1998)

Octocorals produce either isolecithal (e.g. D. hemprichi) or telolecithal eggs (e.g. P.f. fulvum) that undergo holoblastic cleavage (e.g. Benayahu & Loya 1983; Benayahu 1989; Benayahu et al. 1989; Dahan and Benayahu 1998; Uehara et al. 1987; Lasker and Kim 1996). Studies of embryogenesis in octocorals are limited to a small number of shallow-water alcyonaceans and the Pennatulid Ptilosarcus guerneyi (Chia and Crawford 1973). These studies reveal that cleavage in developing embryos may be unequal (e.g. brooding soft coral, P. f. fulvum, Benayahu and Loya 1983) or equal (e.g. Lobophytum crassum, Uehara et al. 1987; Dendronephytha hemprichi, Dahan and Benayahu 1998) with both types of cleavage present in at least one species (Anthelia glauca, Benayahu and Schleyer 1998). Unequal cleavage produces a morula with small cells at the animal pole and larger cells at the vegetal pole with continued division leading to the formation of a solid steroblastula (Benayahu and Loya 1983). In species with equal cleavage, morula have blastomeres of equal size and form a solid blastula (Benayahu 1989). In at least two species of alcyonaceans, Dendronepthya hemprichi and Clavularia hamra, a certain percentage of developing embryos may exhibit alternative development patterns that produce unusually formed embryos (Benayahu 1989; Dahan and Benayahu 1998). Further development of all blastula (both regular and unusually-formed) leads to a smooth gastrula stage (Benayahu and Loya 1983; Benayahu 1989) and subsequent transformation into ciliated planula (Dahan and Benayahu 1998).

The rate of embryogenesis appears to differ between broadcast spawning and brooding octocorals where development of embryos from oviparous octocorals (i.e. broadcast spawners) occurs more rapidly (e.g. A. digitatum, 3-4 days, Matthews 1917; Renilla kollikeri, 2 days, Satterlie and Case 1979) than among viviparous (i.e. brooding) species (e.g. Dendronephthya hemprichi, Benayahu 1989). Benayahu and Loya (1983, 1986) suggest that more rapid embryogenesis in the water column reduces a young coral's exposure time to mortality factors such as elevated predation risk, damage from wave action and resuspended sediments. Embryos brooded in adult tissues are in a more protected environment, allowing for slower embryological development (Kruger et al. 1998).

While there is limited information on larval feeding ability, most octocoral planula appear to be lecithotrophic (Benayahu and Loya 1983; Chia and Crawford 1973 and others). In species with zooxanthellate planula additional nutrition may be acquired through metabolized photosynthetic products (Richmond 1989; Ben-David-Zaslow and Benayahu 1998). No evidence currently exists for uptake of DOM by octocoral planula (Dahan and Benayahu 1998).

Recruitment & Settlement

The length of time from fertilization until larvae achieve competency remains unknown for most species of octocorals. Once larvae become competent to metamorphose they must locate a suitable environment in which to settle. Successful recruitment depends upon encounter and selection of appropriate habitat, thus an ability to delay metamorphosis in the absence of a suitable environment may enhance the probability of survival by increasing the time available to locate more favorable conditions. The energetic resources available to developing larvae have been shown to influence both competency period and metamorphosis (references in Ben-David-Zaslow and Benayahu 1998). Richmond (1989) proposed that planula with zooxanthellae may benefit from nutritive algal metabolites, allowing them to extend their competency period. Contrary to Richmond 's prediction, Ben-David-Zaslow and Benayahu (1998) found no significant difference in competency period or larval longevity between several species of zooxanthellate and azooxanthellate soft corals from the Red Sea . This suggests that for lecithotrophic octocoral larvae, nutrient sources within the oocyte are a key important factor controlling larval competence and longevity, and ultimately dispersal capabilities.

The dispersal abilities of octocoral larvae vary widely, especially among alcyonacean-type octocorals. In brooding species with crawling larvae, settlement occurs in the immediate vicinity of the parent colony (e.g. Alcyonium siderium, Sebens 1983; Capnella gaboensis, Farrant 1986) while brooders with swimming, planktonic larvae may disperse more widely (e.g. Anthomastis ritteri, Cordes et al. 2001; Dendronephthya hemprichi, Dahan and Benayahu 1998). Despite their locomotory abilities, most planular larvae of brooding, shallow-water octocorals appear to settle shortly after release (Brazeau and Lasker 1990; Coma et al. 1995; Excoffen et al. 2004). Observations of newly released larvae have shown that they are negatively buoyant and sink rapidly

(Benayahu and Loya 1983; Brazeau and Lasker 1990; Gutierrez-Rodriguez and Lasker 2004). Benayahu and Loya (1987) proposed that short-range dispersal of planula is a common trait among coral reef alcyonaceans and may enhance localized recruitment and contribute to the patchy distribution of species. This strategy may be advantageous in space-limited environments (such as coral reefs) because larvae are immediately presented with appropriate habitat type in which to settle (Sebens 1983 in Benayahu and Loya 1987). While most larvae of brooding octocorals exhibit rapid settlement behavior, the planula of the Caribbean gorgonian-type octocoral, Pseudopterogorgia elisabethae, appear to be an exception. Gutierrez-Rodriguez and Lasker (2004) noted from field observations that while settlement of some planula occurred in close proximity to the parent colony (<5 m), most planula remained in the water column (presumably due to turbulence) and were even transported to the water surface, increasing the potential for advection from the local environment.

It is generally accepted that the larvae of broadcast spawning octocorals (i.e. Pennatulaceans and some alcyonaceans) have greater dispersal capabilities than brooded larvae, however data on long-distance transport of octocoral planula is lacking. Dahan and Benayahu (1998) reported that the planular larvae of the broadcast spawning alcyonacean, Dendronephytha hemprichi, swim actively and have a relatively long competency period (65 days). Such larval life features "undoubtedly promote a considerable larval transport in the field." (Dahan and Benayahu 1998). The cosmopolitan distribution of some deep-water Pennatulids (e.g. Kophobelemnon stelliferum, Rice et al. 1992; U. lindahli, Tyler et al. 1995) also suggests the potential for widespread dispersal of larvae from broadcast spawning. In addition to deep-water Pennatulaceans, many species of deep-water alcyonaceans display widespread distribution, often covering entire ocean basins despite the intermittent occurrence of suitable hard substrate habitats. However, at the present time very little is known about reproductive processes of deep-water octocorals. Thus, factors contributing to the widespread distribution of many species are unresolved.

Numerous environmental features including substrate, light/dark cues, and water motion may influence coral settlement and successful recruitment. Many species of shallow-water octocoral larvae preferentially settle in shaded microhabitats, such as the underside of settlement plates (Alino and Coll 1989; Zeevi Ben-Yosef and Benayahu 1999; Benayahu and Loya 1987; Dahan and Benayahu 1997 and others). This settlement behavior may be an avoidance response to conditions that exist on the upper surface of a plate, such as high light intensity, low tides, competition from filamentous algae, grazing pressure, and sedimentation (Rogers et al. 1984 in Benayahu and Loya 1987; Benayahu and Loya 1984b). Despite potential unfavorable conditions that may exist on exposed surfaces, Alino and Coll (1989) observed reduced survivorship of larvae among the tropical alcyonaceans Lobophytum crassum and Sinularia conferta resident on the undersides of settlement plates compared to the light-exposed surfaces. The general trend toward settlement in shaded microhabitats appears to decrease with increasing depth (Benayahu and Loya 1987), presumably due to both reduced competition with algae and lowered grazing pressure. Thus, it stands to reason that, in deeper waters, substrate and water motion are key factors influencing octocoral planula settlement. In

addition to settlement in shaded microhabitats, alcyonacean larvae exhibited a preference for substrates with turf or crustose coralline algae, rough surfaces, and pits in the substrata (Benayahu and Loya 1984b). Water flow may also be an important factor influencing larval settlement. Benayahu and Loya (1987) reported that settlement in Red Sea alcyonacean coral, X. macrospiculata, occurred predominantly along the edges of deployed settlement plates, a pattern which may be related to regions of low flow associated with turbulent eddies created as water travels over the plates (references in Benayahu and Loya 1987).

Once an octocoral planula locates an appropriate location to settle it undergoes metamorphosis to a feeding polyp. This process involves secretion of mucus for temporary attachment to the substrate during settlement (Benayahu and Loya 1983; and others). There are few reports of larval metamorphosis in octocorals. In the alcyonacean soft coral, P. f. fulvum, attachment to the substrate is followed by development into a cone-shaped polyp with 8 tentacular buds. Within a week to ten days, the tentacles elongate and septa develop inside the polyp. In successive weeks tentacles development pinnules and within the next month additional polyps are added and sclerites are present in the polyps (Benayahu and Loya 1983). Similar processes settlement and metamorphosis have been observed in the alcyonacean soft corals Capnella gaboensis (Farrant 1986) and X. macrospiculata (Benayahu and Loya 1984).

A limited number of studies indicate that successful settlement and recruitment into a population occurs at a low rate, at least among shallow-water alcyonacean octocorals (Farrant 1987; Grigg 1977; Lasker et al. 1998). Farrant (1987) reported that for the temperate soft coral, Capnella gaboensis, the first year survival rate of newly settled colonies was 0.26%. Similarly, for the broadcast spawning alcyonacean, Plexaura kuna, Lasker et al. (1998) estimated annual survival of new colonies at 10-6. Using a Poisson probability distribution, Lasker et al. (1998) calculated that in order to produce a successful a recruitment event 95% of the time, that settlement of 700,000 individuals per year would be required. Their calculated mortality rate for P. kuna settlers of 3% per day yields an extremely low probably for successful recruitment, suggesting that this species may rely on certain environmental circumstances that enhance successful recruitment (e.g. favorable substrata, Gotelli 1988; reduced grazing, Yoshioka 1996). Extremely high post-settlement mortality of new recruits implies that successful settlement may be more closely tied to water column and post-settlement survival than to gamete production and fertilization rates (Lasker et al. 1998). Coffroth and Lasker (1998b) proposed that the life history strategy of P. kuna relies on “large and long-lived genets” which may only achieve successful sexual reproduction very infrequently over the course of the colonies’ multi-decadal lifespan. There is evidence that many species, especially those in deep and temperate waters, are long-lived (Andrews et al. 2002; Risk et al. 2002) and therefore may possess similar reproductive life history characteristics.